

"Lost in time" but still moving to the beat

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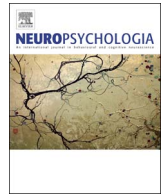
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“Lost in time” but still moving to the beat

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ABSTRACT

Motor synchronization to the beat of an auditory sequence (e.g., a metronome or music) is widespread in humans. However, some individuals show poor synchronization and impoverished beat perception. This condition, termed “beat deafness”, has been linked to a perceptual deficit in beat tracking. Here we present single-case evidence (L.A. and L.C.) that poor beat tracking does not have to entail poor synchronization. In a first Experiment, L.A., L.C., and a third case (L.V.) were submitted to the Battery for The Assessment of Auditory Sensorimotor and Timing Abilities (BAASTA), which includes both perceptual and sensorimotor tasks. Compared to a control group, L.A. and L.C. performed poorly on rhythm perception tasks, such as detecting time shifts in a regular sequence, or estimating whether a metronome is aligned to the beat of the music or not. Yet, they could tap to the beat of the same stimuli. L.V. showed impairments in both beat perception and tapping. In a second Experiment, we tested whether L.A., L.C., and L.V.’s perceptual deficits extend to an implicit timing task, in which they had to respond as fast as possible to a different target pitch after a sequence of standard tones. The three beat-deaf participants benefited similarly to controls from a regular temporal pattern in detecting the pitch target. The fact that synchronization to a beat can occur in the presence of poor perception shows that perception and action can dissociate in explicit timing tasks. Beat tracking afforded by implicit timing mechanisms is likely to support spared synchronization to the beat in some beat-deaf participants. This finding suggests that separate pathways may subserve beat perception depending on the explicit/implicit nature of a task in a sample of beat-deaf participants.

1. Introduction

One of the most compelling reactions to music is to move to its beat. Humans spontaneously or intentionally tend to clap their hands, sway their body, or tap their feet to the beat of music. Synchronizing movement to the beat (Repp, 2005; Repp and Su, 2013) involves the coordination of a discrete action with a sequence of rhythmic auditory events (e.g., tones of a metronome or musical beats). This complex activity is supported by a neuronal network, including areas devoted to tracking the musical beat (e.g., the basal ganglia; Grahn and Brett, 2007; Grahn and Rowe, 2009) and motor coordination (e.g., the cerebellum; Coull, Cheng, and Meck, 2011; Grube et al., 2010;

Schwartz and Kotz, 2013). Motor synchronization to the beat is likely to be hard-wired as it appears spontaneously and early during development (Drake et al., 2000; Kirschner and Tomasello, 2009; Phillips-Silver and Trainor, 2005). Accordingly, this skill is highly widespread in the general population (Repp, 2010; Sowiński and Dalla Bella, 2013).

Even though the majority can move to the beat of music, some individuals, referred to as “beat-deaf” (Palmer et al., 2014) encounter particular difficulties in synchronizing to the beat (see also Sowiński and Dalla Bella, 2013). This condition is considered to be a congenital anomaly in the absence of brain damage (Phillips-Silver et al., 2011; Sowiński and Dalla Bella, 2013). An example of beat deafness is the

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case of Mathieu (Phillips-Silver et al., 2011), a young man who was unable to bounce accurately to the beat of music while showing good synchronization to a simple metronome. His poor synchronization is likely to result from poor perception, as he was inaccurate in estimating whether a dancer is on or off the beat in a music video. Notably, Mathieu's deficits cannot be ascribed to a general impairment of music processing (e.g., Peretz and Hyde, 2003; Stewart, 2008; see also Dalla Bella and Peretz, 2003). His pitch perception is spared as tested with the Montreal Battery of the Evaluation of Amusia (MBEA; Peretz et al., 2003).

The case of Mathieu points toward a perceptual explanation of poor synchronization to the beat. Inaccurate extraction of the beat from complex auditory signals (e.g., music), including several periodicities at different embedded temporal scales (meter; London, 2012), may bring about poor synchronization (Phillips-Silver et al., 2011). This deficit may not be apparent with a simpler isochronous sequence (e.g., a metronome) though. Beat tracking with a metronome is still possible, while beat extraction and synchronization with metrical rhythms are impaired (Launay et al., 2014). However, inaccurate beat perception is not mandatory to explain poor synchronization to the beat. In a large-scale study with around 100 students that were tested with a battery of rhythm perception and paced tapping tasks, we reported two cases (S1 and S5) who exhibited poor synchronization to the beat while showing spared rhythm perception (Dalla Bella and Sowiński, 2015; Sowiński and Dalla Bella, 2013). Additional evidence of sensorimotor deficits in beat deafness was provided more recently by Palmer and collaborators (Palmer et al., 2014). They showed that two beat-deaf participants, including Mathieu, had difficulties in adapting their tapping to perturbations in an isochronous sequence, next to poor beat perception. Finally, a recent study (Mathias et al., 2016) reports that Mathieu but not Marjorie, another beat-deaf participant, showed an abnormal P3 response to the omission of a beat in a musical sequence. Altogether these data suggest that there are different individual profiles of beat deafness, depending on the impairment of beat perception and/or production.

The dissociation between beat perception and tapping to the beat that we reported in two poor synchronizers (Sowiński and Dalla Bella, 2013) is particularly intriguing. It suggests that perception and action in the rhythm domain may be partly independent. However, task factors such as difficulty, attention, and memory demands may explain these differences. For example, synchronization requires both tracking the beat and generating a motor response. Thus, it may be more demanding than a simple perceptual task. As the opposite dissociation - impaired beat perception with spared synchronization - has not been described so far, it is difficult to conclude whether there are two independent mechanisms involved. However, a functional separation of perception and action is not unusual, and is supported by a double dissociation in pitch processing (for reviews, see Dalla Bella et al., 2011; Berkowska and Dalla Bella, 2009; Dalla Bella, 2016). A similar functional architecture may apply to rhythm. Beat perception and synchronization to the beat involve multiple components, which may be difficult to dissociate in the healthy brain, as motor and perceptual processes are usually strongly coupled (Grahn, 2012; Kotz et al., 2016; Repp, 2005; Repp and Su, 2013). Yet, first evidence that these processes can be disrupted separately as a result of brain damage or a developmental disorder (Fries and Swihart, 1990; Provasi et al., 2014; Sowiński and Dalla Bella, 2013) suggests some degree of functional separability.

Our goal is to present two cases of beat deafness (L.A. and L.C.) and to show that poor beat perception can occur while synchronization to the beat is spared. A third case, L.V. displays impairment of both beat perception and synchronization. With these data we also confirm the sensitivity of a battery of timing tests to detect both perceptual and synchronization deficits. In a first Experiment, participants' beat perception and synchronization to the beat were assessed with the Battery for The Assessment of Auditory Sensorimotor and Timing

Abilities (BAASTA; Dalla Bella et al., 2016; see also Benoit et al., 2014; Falk et al., 2015). An additional question was whether deficits in beat tracking observed in explicit timing tasks (e.g., Fujii and Schlaug, 2013; Phillips-Silver et al., 2011; Repp and Su, 2013; Repp, 2005; Sowiński and Dalla Bella, 2013) extend to implicit timing processes. In general, explicit timing is associated with tasks requiring either voluntary motor production (e.g., synchronized tapping tasks; Repp, 2005), or perceptual discrimination of a timed duration (e.g., anisochrony detection, Ehrlé and Samson, 2005; Hyde and Peretz, 2004). In contrast, implicit timing is involved in tasks that do not explicitly test timing (e.g., detecting a deviant pitch in a temporally regular or irregular sequence), but in which temporal prediction affects performance (Coull, 2009; Coull and Nobre, 2008; Nobre et al., 2007; Sanabria et al., 2011). In particular, temporal prediction fostered by a regular temporal pattern of sensory stimuli improves performance in these tasks (e.g., reduces reaction times; Lange, 2010; Sanabria et al., 2011; Sanabria and Correa, 2013). Explicit and implicit timing are associated with distinct neuronal substrates, involving cortico-striato-cortical networks and inferior parietal-premotor networks with projections from the cerebellum, respectively (Coull and Nobre, 2008; Coull et al., 2011; Kotz and Schwartz, 2010; Nobre and Coull, 2010; Schwartz and Kotz, 2013; Zelaznik et al., 2002). Here we hypothesize that beat perception deficits characteristic of beat deafness as observed in explicit tasks may not carry over to implicit timing tasks. This hypothesis was tested in a second Experiment, in which L.A., L.C., and L.V. were asked to respond as quickly as possible to a target sound presented either after five sounds embedded in a temporally regular or an irregular sequence. Better performance following the regular sequence of sounds compared to the irregular sequence would be indicative of spared implicit timing processing.

2. Experiment 1

2.1. Participants

2.1.1. Cases histories

L.A., L.C., and L.V. were 21-year-old female university students recruited at the University of Montpellier. L.A. and L.V. had not received any musical training. L.C., in spite of the fact that she received 5 years of non-formal piano lessons, considers herself a non-musician. She practiced less than 1 h a week during her musical training, and has rarely played the piano in the last 7 years. L.V. complained about difficulties in finding the beat in music, especially while dancing, singing, or tapping the foot to the beat. In contrast, L.C. and L.A. reported no difficulties with beat tracking. Neither participant suffered from a brain injury nor had undergone brain surgery. None of them reported previous neurological or psychiatric problems or an auditory deficit.

2.1.2. Control group

Seven female university students recruited at the University of Montpellier, matched to the three beat-deaf participants took part in the study. They were between 18 and 30 years old ($M=23.29$ years; $SD=4.54$), and were self-reported non-musicians (mean number of years of musical training=1.29; $SD=1.89$). They did not have any previous neurological or psychiatric problems. All participants provided informed consent for participating in the study.

2.2. Material and method

The participants were submitted to BAASTA (Dalla Bella et al., 2016) as a way to assess their explicit perceptual and sensorimotor timing abilities. In addition, they performed the pitch-related tasks of the MBEA (Contour, Interval, and Scale subtests; Peretz et al., 2003) to assess their pitch perception.

2.2.1. Assessment of timing skills: BAASTA

The battery includes 8 tasks divided in 2 parts, 4 perceptual tasks, and 4 sensorimotor tasks, described below.

Perceptual timing tasks are *Duration discrimination*, *Anisochrony detection with tones*, *Anisochrony detection with music*, and the *Beat Alignment Test*.

Duration discrimination: This task tests duration discrimination. Two tones (frequency=1 kHz) are presented successively. The first one lasts 600 ms (standard duration), while the second lasts between 600 and 1000 ms (comparison duration). Participants judge whether the second tone lasted longer than the first.

Anisochrony detection with tones: The goal of this task is to test participants' ability to detect a time shift in an isochronous tone sequence. Sequences of 5 tones (1047 Hz, tone duration=150 ms) are presented with a mean Inter-Onset Interval (IOI) of 600 ms. Sequences can be isochronous (i.e., with a constant IOI) or not (the 4th tone is presented earlier than expected by up to 30% of the IOI). Participants judge whether the sequence is regular or not.

Anisochrony detection with music: This task is the same as Anisochrony detection with tones, but uses a musical sequence, namely an excerpt of two bars from Bach's "Badinerie" orchestral suite for flute (BWV 1067) played with a piano timbre. The music's Inter-Beat Interval (IBI) is 600 ms. As before, the IBI can be constant (regular) or not (irregular; the 4th beat occurs earlier than expected by up to 30% of the IBI). Participants judge whether the sequence is regular or not.

Beat Alignment Test: The objective of this task is to assess participants' beat perception. Stimuli ($n=72$) are based on 4 regular musical sequences, including 20 beats each (beat = quarter note). Two sequences are fragments from Bach's "Badinerie", and 2 from Rossini's "William Tell Overture", played with a piano timbre. Stimuli are played at three different tempos (with 450-, 600-, and 750-ms IBIs). Starting with the 7th musical beat, a metronome (i.e., isochronously presented triangle sounds) is superimposed onto the music in 2 conditions: aligned with the beat or non-aligned. In the non-aligned condition, the metronome is either phase shifted (the sounds are presented before or after the musical beats by 33% of the music IBI, while keeping the tempo), or period shifted (the tempo of the metronome changes by more or less 10% of the IBI). Participants judge if the metronome is aligned or not with the musical beat.

The perceptual timing tasks were implemented using Matlab software (version 7.6.0). In the first 3 tasks, a maximum-likelihood adaptive procedure (MLP) (Green, 1993; MATLAB MLP toolbox, Grassi and Soranzo, 2009) was used to obtain perceptual thresholds (Benoit et al., 2014). All tasks were preceded by 4 examples and 4 practice trials with feedback.

Sensorimotor timing tasks are *Unpaced tapping*, *Paced tapping to an isochronous sequence*, *Paced tapping to music*, *Synchronization-continuation* and *Adaptive tapping*.

Motor and sensorimotor timing skills are tested with finger tapping tasks. Participants respond with their dominant hand.

Unpaced tapping: The purpose of this task is to obtain a measure of the participants' preferred tapping rate, and its variability in the absence of a pacing stimulus. Participants are asked to tap at their most natural rate for 60 s.

Paced tapping with an isochronous sequence: The goal of this task is to assess synchronization with a metronome (i.e., a sequence of isochronously presented tones). Participants tap with their index finger to a sequence of 60 piano tones (frequency=1319 Hz) at 3 different tempos (600-, 450- and 750-ms IOI). The task is repeated twice, and is preceded by one practice trial.

Paced tapping with music: This task is similar to the previous one, but uses music as a pacing stimulus. Participants tap to the beat of two musical excerpts taken from Bach's "Badinerie" and Rossini's "William Tell Overture". Each musical excerpt contains 64 quarter notes (IBI=600 ms). The task is repeated twice for each excerpt, and is preceded by one practice trial.

Synchronization-continuation: In this task the ability to continue tapping at the rate provided by a metronome is tested. Participants synchronize with an isochronous sequence (10 tones), and continue tapping at the same rate after the sequence stops, for a duration corresponding to 30 IOIs of the pacing stimulus. Isochronous sequences are provided at three tempos (600-, 450-, and 750-ms IOI). The task is repeated twice at each tempo, and is preceded by one practice trial.

Adaptive tapping: The aim of this last task is to assess the ability to adapt to a tempo change in a synchronization-continuation task. As done in the previous task, participants tap to an isochronous sequence (10 tones), but at the end of the sequence (last 4 tones) the tempo either increases, decreases, or remains constant (40% of the trials). Tempo change is either 30 or 75 ms. The task is to tap to the tones in the sequence, to adapt to the tempo change, and to keep tapping at the new tempo after the stimulus stops for a time corresponding to 10 IOIs. After each trial, participants judge whether they perceived a change in stimulus tempo (acceleration, deceleration, or no change). Trials are divided into 10 experimental blocks (6 trials x 10 block overall), and presented in random order. A training block precedes the first experimental trial.

In all the sensorimotor tasks, the performance was recorded via a Roland SPD-6 MIDI percussion pad. Stimulus presentation and response recording was controlled by MAX-MSP software (version 6.0). Stimuli were delivered over headphones (Sennheiser HD201).

The tasks were administered in the order presented above. The whole battery lasted between 1 h and a half to 2 h.

2.2.2. Assessment of pitch perception: MBEA

To assess pitch perception of the three beat-deaf participants and to rule out the possibility of congenital amusia, participants were submitted to the three tasks of the MBEA focusing on pitch perception (Peretz et al., 2003): Contour, Interval, and Scale subtests.

2.3. Analysis

2.3.1. BAASTA

2.3.1.1. Perceptual timing. For Duration discrimination, Anisochrony detection with tones and with music, mean thresholds across the three blocks were calculated. The blocks including more than 30% of False Alarms (FAs) were rejected. A FA was scored when the participant reported a difference in duration, or that the sequence beat was irregular, while there was no difference/no deviation from isochrony in the stimulus. The threshold is expressed in percentage of the standard duration in the three tasks (Weber fraction).

In the BAT, we calculated the sensitivity index (d') for the 3 tempos (slow, medium, and fast). d' was calculated on the basis of the number of Hits (when a misaligned metronome was correctly detected) and FAs (when a misalignment was erroneously reported). We also computed the error rate separately for phase and period changes.

2.3.1.2. Sensorimotor timing. Mean inter-tap interval (ITI, in ms) and motor variability (coefficient of variation of the ITI - CV ITI - namely, the SD of the ITI/mean ITI) were computed for Unpaced tapping and for the Synchronization-continuation tasks. Synchronization in the Paced tapping task was analyzed using circular statistics (Fisher, 1993; Circular Statistics Toolbox for Matlab, Berens, 2009). Circular statistics are particularly appropriate for analyzing synchronization performance in the general population, and show high sensitivity to individual differences in both healthy and patient populations (Dalla Bella et al., 2015; Dalla Bella and Sowiński, 2015; Falk et al., 2015; Kirschner and Tomasello, 2009; Woodruff Carr et al., 2014). The method consists in representing the taps as unit vectors with a given angle on a 360° circular scale. The full circle represents the inter-

stimulus interval (e.g., beats or tones). The mean resultant vector R is calculated based on the unit vectors corresponding to all the taps in a sequence. To assess whether participants' performance was above chance, data were submitted to Rayleigh's test for circular uniformity (Fisher, 1993; Wilkie, 1983). Synchronization performance was assessed by considering the length of vector R , which indicates whether the taps were systematically occurring before or after the pacing stimuli (*synchronization consistency*). This value ranges between 0 and 1, with 1 indicating maximum consistency (no variability), and 0, a random distribution of angles around the circle (i.e., lack of synchronization). Synchronization consistency has shown high sensitivity to individual differences in synchronization skills and can be used to uncover poor synchronizers (e.g., Dalla Bella and Sowiński, 2015; Fujii and Schlaug, 2013; Sowiński and Dalla Bella, 2013; Woodruff Carr et al., 2014).

Finally, the data from the Adaptive tapping task were analyzed by calculating an adaptation index (Schwartz et al., 2011). This method consists in fitting a regression line to the slopes of ITIs function of the final sequence tempo; the value of the slope corresponds to the adaptation index. When the value is 1, the adaptation is perfect; lower and higher values than 1 indicate undercorrection and overcorrection, respectively. This index was calculated separately for tempo acceleration (i.e., faster tempos with final sequence IOIs < 600 ms) and tempo deceleration (slower tempos with final sequence IOIs > 600 ms). The sensitivity index (d') for detecting tempo changes was also computed based on the number of Hits (when a tempo acceleration or deceleration was correctly detected) and FAs (when a tempo acceleration or deceleration was reported while there was no change or the opposite change).

2.3.2. MBEA

A pitch composite score was computed for the MBEA, averaging the results from the three pitch tasks (maximum performance in each task=30). The scores of the three beat-deaf individuals were compared to the normative data from a comparable group of 100 participants (Cuddy et al., 2005).

2.3.3. Single-case statistics

In order to determine whether the three beat-deaf participants performed poorly on the aforementioned tasks, their performance was compared to cut-off scores obtained from controls for each variable using statistics adapted for the analysis of single cases (*Singlims* program, Crawford and Garthwaite, 2002; Crawford and Howell, 1998). Thresholds for all the tasks are provided in Table 1. In addition, the Revised Standardized Difference Test (RSDT, Crawford and Garthwaite, 2005; Garthwaite and Crawford, 2004) was used to confirm the dissociations between perception and action previously found in explicit timing tasks for L.A. and L.C. RSDT compares the difference between the results obtained in two tasks for one participant relative to the performance of a matched control group, while controlling for Type I error.

2.4. Results

2.4.1. BAASTA

2.4.1.1. Perceptual timing tasks. The results of the perceptual tasks of the BAASTA are shown in Fig. 1¹. Perceptual thresholds for Duration discrimination, Anisochrony detection with tones and music, and d' values and error rates for the BAT are reported. In the Duration discrimination task, all three blocks were discarded for L.V. and for two

controls (i.e., for them, there was no valid estimation of the threshold), two blocks were removed for two controls, and one block for one additional control participant. In the Anisochrony detection task with a metronome (600 ms), one block was discarded for two controls. Finally, in the Anisochrony detection task with music one block was removed for L.V. and for three controls. Removal of all these blocks was due to an excess of FAs. For L.A., thresholds could not be reliably computed using the MLP procedure, due to the inconsistency of her responses. In addition, she was unable to distinguish between the examples during the practice trials, in spite of the fact that maximum duration differences (60% of the intervals) were presented. L.A. exhibited very poor detection of misaligned beats in the BAT (i.e., very low d'), and a higher error rate for both period and phase change trials than controls. L.C. showed poorer performance than controls in the Anisochrony detection task with tones and in the BAT (higher error rate for phase changes). She also obtained a particularly high detection threshold in the Duration discrimination task, but this result was not confirmed when the task was repeated (threshold=17.31). Finally, L.V. exhibited difficulties in detecting anisochronies with tones and showed poor detection of aligned beats in the BAT (lower d' for fast and slow trials, higher error rates for both period and phase changes).

2.4.1.2. Sensorimotor timing tasks. The results obtained by beat-deaf participants and controls in Unpaced and Paced tapping tasks are presented in Fig. 2. The three beat-deaf participants showed motor variability comparable to controls in the Unpaced tapping task. In addition, L.A. and L.C.'s spontaneous motor tempo (ITI=681.10, 717.74 ms, respectively) did not differ from that of controls (mean ITI=563.71, $SD=88.64$). Only L.V.'s spontaneous tapping rate (ITI=913.84 ms) was significantly slower as compared to controls ($t(6)=3.26$, $p < .01$).

The results in the Paced tapping tasks showed that the beat-deaf participants were well above chance, as assessed by the Rayleigh's test, except for L.V., who could not synchronize with musical stimuli. L.A. and L.C. were as consistent as controls in synchronizing to both a metronome and to music. L.V., in contrast, was less consistent than controls when tapping to isochronous sequences (with 450-ms ms and 750-ms IOIs), and to music.

The results of the Adaptive tapping task are reported in Fig. 3. As can be seen, L.A. and L.C. performed poorly in the perception part of the task. Their performance was worse than that of controls in detecting small tempo accelerations (~30% of the IOI). In contrast, all three beat-deaf participants were capable to adapt their tapping to the tempo change like controls did, as shown by the adaptation indexes.

Results in the Synchronization-continuation task from the three beat-deaf participants were comparable to controls' performance. Mean motor variability in the continuation phase (CV of the ITIs) for the control group was .03 (range=.02–.06), and .04, .06, and .05 for L.A., L.C. and L.V., respectively.

2.4.1.3. Dissociation between perception and action. RSDT confirmed that perception and action dissociated in L.A. and L.C., showing impaired perception in the presence of spared synchronization relative to controls. Differences were found when comparing Anisochrony detection with tones and Paced tapping with a metronome for L.C. ($t(6)=13.73$, $p < .0001$). In addition, a comparison of the BAT (error rate) and Paced tapping with music (consistency) showed a significant dissociation of the two tasks for both L.A. (error rate, phase: $t(6)=8.05$, $p < .0001$; error rate, period: $t(6)=4.24$, $p < .001$) and L.C. (error rate, phase: $t(6)=6.66$, $p < .0001$; error rate, period: $t(6)=4.03$, $p < .001$). Finally, in Adaptive tapping, a dissociation was found between perception (d') and synchronization

¹ In order to confirm that L.A. and L.C.'s deficits in perceptual tasks were not due to an effect of practice, these participants were tested a second time on these tasks. All the results were confirmed except the deficit in Duration discrimination for L.C.

Table 1

Cut-off scores in the tasks of the BAASTA based on the performance of the control group.

Task	Variable	Cut-off
Duration Discrimination	Threshold (Weber fraction)	32.96
Anisochrony Detection with tones	Threshold (Weber fraction)	13.30
Anisochrony Detection with music	Threshold (Weber fraction)	21.78
Beat Alignment Test	d' (slow tempo)	1.96
	d' (medium tempo)	1.20
	d' (fast tempo)	1.24
	% of errors (phase change)	12.17
	% of errors (period change)	33.28
Unpaced tapping	Motor Variability	.09
Paced tapping	Consistency (tones, slow tempo)	.89
	Consistency (tones, medium tempo)	.72
	Consistency (tones, fast tempo)	.89
	Consistency (music)	.89
Adaptive tapping	d' (acceleration, -75% IOI)	2.31
	d' (acceleration, -30% IOI)	1.12
	d' (deceleration, +30% IOI)	1.14
	d' (deceleration, +75% IOI)	1.66
	Adaptation index (acceleration)	.49
	Adaptation index (deceleration)	.25

(adaptation index for deceleration) in L.A. ($t(6)=1.94$, $p < .05$).**2.4.2. MBEA**

The pitch-composite scores obtained in the MBEA for L.A., L.C., and L.V. were 25.3, 27.0, and 25.3, respectively. These scores are well above the threshold for pitch perception deficits (20.1) from a

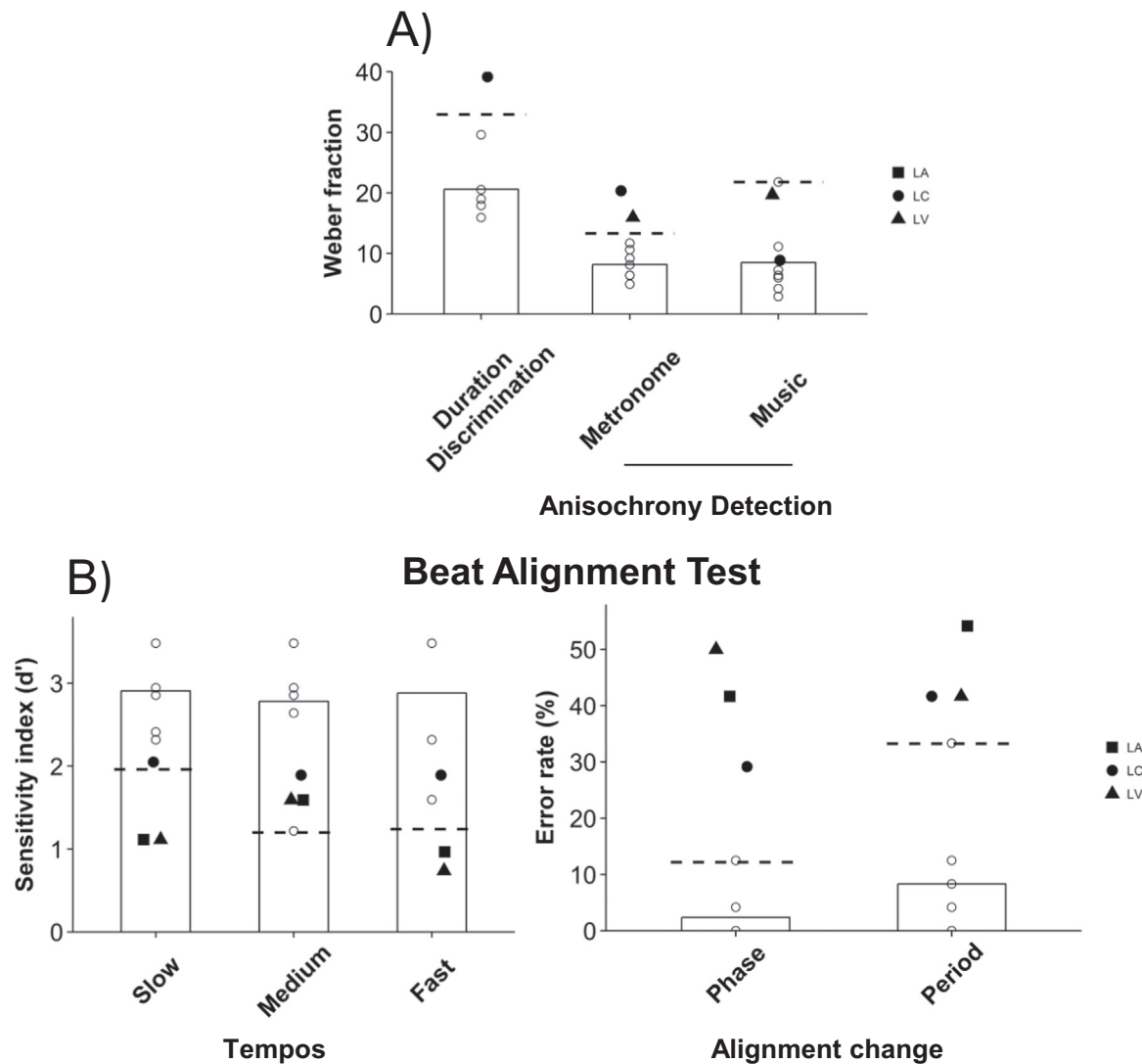


Fig. 1. Results obtained by L.A., L.C., and L.V. and by matched controls in A) Duration discrimination, Anisochrony detection with tones and music, and B) the BAT. Unfilled circles indicate controls' individual performances and bars represent controls' means. Dotted lines indicate the cut-off score.

comparable age group (Cuddy et al., 2005).

2.5. Discussion

In this first Experiment, we submitted three beat-deaf participants, L.A., L.C., and L.V. and a control group to an exhaustive battery of perceptual and sensorimotor timing tasks. The results of L.A. and L.C. indicate a dissociation between perception and action in explicit timing tasks. They both performed poorly when asked to detect a shift in an isochronous sequence, with thresholds above 14% of the interval between the tones. L.C. was also unable to judge whether a repeated tone was aligned or not to the musical beat. This is rather surprising as she was perfectly able to tap to the beat of the same excerpts. Indeed, in spite of their poor beat perception, L.A. and L.C. could synchronize to the beat of both simple and complex (i.e., musical) auditory sequences. Note that L.A. was very consistent in tapping to the beat. In addition, L.A. and L.C. could tap at a spontaneous tempo in the absence of a pacing stimulus comparable to controls. The performance in the Adaptive tapping task is particularly critical to test the relation between perception and action. The task requires both a perceptual judgment of a change in the stimulus rate, and a motor adaptation to this change during synchronization. Interestingly, both L.A. and L.C. exhibited

difficulties in the perceptual judgment, while they were fully capable to adapt to the change in tapping. Finally, the beat-deaf participants exhibited unimpaired pitch perception, as shown by the MBEA, which confirms that they were not tone-deaf.

Beat deafness was originally described as an impairment in beat processing, both in perception and performance (Palmer et al., 2014; Phillips-Silver et al., 2011). Impaired beat tracking and poor synchronization was found in L.V. showing that the tasks used in the present study (BAASTA battery) are sensitive to disorders in rhythm processing previously described in the literature. Some of the tasks of BAASTA were used in a previous study to pinpoint individual differences in timing skills in the general population (Sowiński and Dalla Bella, 2013). In that study, some individuals showed poor synchronization to the beat with or without poor beat perception. Here, we report for the first time two cases (L.A. and L.C.) presenting the opposite pattern of impairment, namely poor beat perception with spared synchronization across various tasks. This finding may appear paradoxical, as we may expect that difficulties in beat tracking or in perceiving shifts in a regular sequence in explicit tasks negatively impinge on synchronization. The fact that beat-deaf participants can move to the beat suggests that temporal information, which cannot be overtly treated, may still be processed implicitly, and thereby subserves synchronization to the

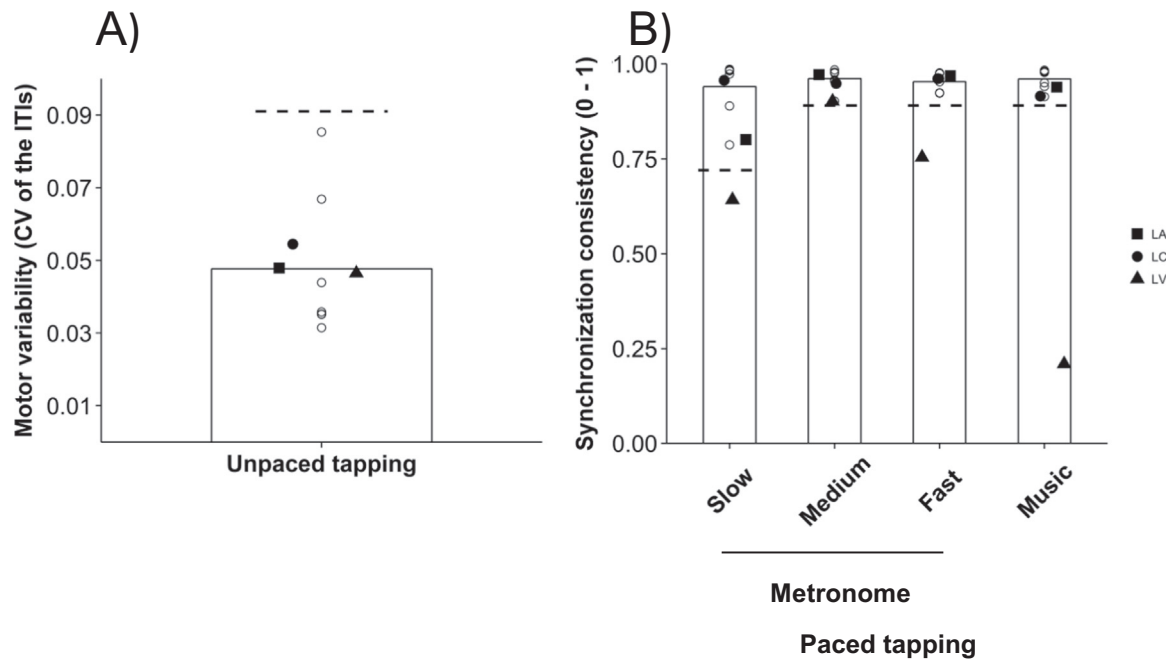


Fig. 2. Results obtained by L.A., L.C., and L.V. and by matched controls in the tapping tasks of BAASTA (A – Unpaced tapping; B – Paced tapping).

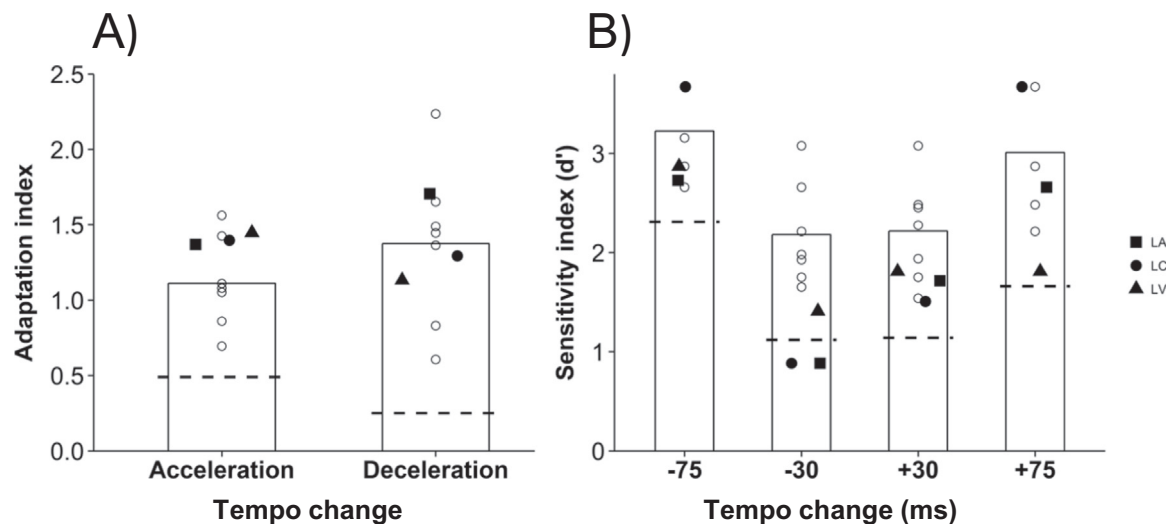


Fig. 3. Results obtained by L.A., L.C., and L.V. and by matched controls in the Adaptive tapping task of BAASTA (A – adaptation index; B – performance in the tempo change detection task).

beat. Implicit timing skills have not been tested so far in beat deafness. The possibility that covert timing skills may be spared in beat-deaf participants was therefore tested in Experiment 2 using an implicit timing task.

3. Experiment 2

3.1. Methods

3.1.1. Participants

The three beat-deaf participants tested in Exp. 1 (L.A., L.C. and L.V.) participated in Exp. 2. Five age-matched participants (3 females) who did not take part in Exp. 1² formed the control group (mean age:

25 years, *SD*: 3.39, range: 20–28).

3.1.2. Material and procedure

The implicit timing task is an adaptation of the classical temporal orienting task, as illustrated in Fig. 4. The task consists in responding as fast as possible to a 50-ms target sound (pitch=400 Hz) presented after a sequence of six 50-ms tones (pitch=700 Hz). Participants were instructed to focus on the target sound without paying attention to the preceding sequence. The sequence preceding the target was either regular or irregular. In the regular sequence the IOI between the tones was constant (550 ms), while in the irregular sequences, the IOI was pseudo-randomly distributed around the mean of 550 ms (IOI range=150, 350, 550, 750, or 950 ms). The target sound was always displayed for 1100 ms (2×IOI) after the last sound of the preceding sequence. There were 240 trials (120 regular and 120 irregular trials) divided in 4 blocks of 60 trials each. Regular and irregular trials were presented in random order in each block. One block lasted 7 min, with

² Controls were submitted to BAASTA to ensure that their explicit timing skills were unimpaired. Their results were comparable to those of the control group in the first Experiment.

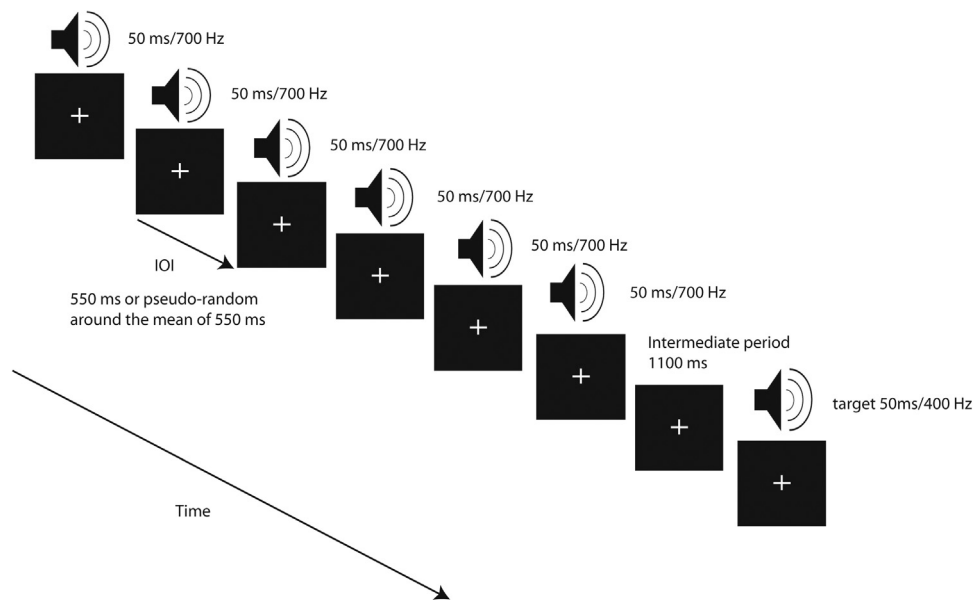


Fig. 4. Schema of the implicit timing task.

a 1 min break between the blocks. The task was implemented in E-Prime 1.0 software (Psychology Software Tools, Pittsburgh, PA).

3.2. Results

Mean reaction times (RT, in ms) in the regular and in the irregular conditions were computed for L.A., L.C., L.V., and for control participants. Differences between the irregular and the regular conditions are reported in Fig. 5. RTs for regular sequences ($M=247.43$, $SD=39.99$) were lower than for irregular sequences ($M=269.15$, $SD=36.99$) for the control group ($t(4)=6.88$, $p<.01$). Similar to Exp. 1, the performance of the three beat-deaf participants was compared to that of controls using single-case statistics with the *Singlims* program (Crawford and Garthwaite, 2002; Crawford and Howell, 1998). No differences were found between the three beat-deaf participants and the control group, suggesting that they similarly benefited from the regularity in the preceding sequence.

3.3. Discussion

The results obtained in the implicit timing task showed beneficial

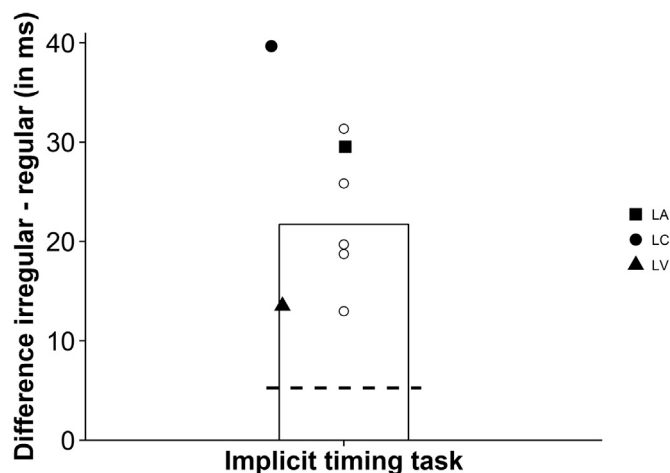


Fig. 5. Individual results obtained from L.A., L.C., and L.V. and from the controls in the implicit timing task.

effects of temporal regularity of the sequence preceding target detection. Reaction times to a target were faster when a regular sequence was presented before the target rather than an irregular one. This finding is consistent with previous results obtained in the same task (Cutanda et al., 2015; De la Rosa et al., 2012). Exp. 2 showed that despite the fact that L.A., L.C., and L.V. had difficulties in performing explicit timing tasks, they could still track the beat covertly, and benefitted from regularity in a reaction time task. As the beat-deaf participants were sensitive to the temporal regularity of a sequence in a perceptual task, implicit timing processes may provide sufficient information to synchronize to the beat.

It has been suggested that explicit and implicit dimensions of timing engage distinct processes, which can be dissociated. Zelaznik et al. (2002) showed that performing a continuous movement task (i.e., circle drawing) relies on an emergent, implicitly controlled timing mechanism that is independent of an explicit temporal representation of durations in tasks such as tapping or duration discrimination. Accordingly, implicit and explicit timing are likely to be supported by different neuronal substrates (Coull and Nobre, 2008; Coull, Cheng, and Meck, 2011). Whereas basal ganglia activity is typically observed in explicit timing tasks with co-activation of other brain regions depending on the task (e.g., pre-SMA, right inferior cortex in duration discrimination), implicit timing and temporal prediction recruit more parietal (e.g., left inferior parietal) and pre-frontal (pre-motor areas) cortical regions as well as the cerebellum (Ivry and Keele, 1989; Schwartz and Kotz, 2013). Thus, the present findings are in line with the existing literature on implicit and explicit timing, and provide first evidence that they can dissociate in beat deafness.

However, it is worth noting that there is growing evidence in favor of a common internal representation of duration in both explicit and implicit timing tasks (Piras and Coull, 2011). A shared internal representation seems to contrast the reported discrepancy between explicit and implicit timing in beat deafness. Still, our findings are not incompatible with the idea that an internal representation of duration is eventually spared, as beat-deaf participants can use it covertly in the implicit timing task. Beat deafness may result from a deficit in the conscious access to a spared representation of duration, leading to poorer performance in explicit beat-tracking tasks. This possibility is discussed in more depth in the General discussion.

4. General discussion

Here we presented two cases of beat deafness (L.A. and L.C.) showing that poor beat perception can co-occur with spared synchronization to the beat. A third case (L.V.) displayed severe timing deficits encompassing perception and action. L.A. and L.C. showed poor perception of changes in regular auditory periodic sequences, or in judging whether a metronome is aligned or not to the beat of music. In spite of poor perception, however, they could tap to the beat of the same stimulus. To the best of our knowledge, this dissociation is reported here for the first time. These findings are reminiscent of the dissociation between perception and action found on the pitch dimension (in tone-deafness and poor-pitch singing; Berkowska and Dalla Bella, 2013; Dalla Bella et al., 2011; Dalla Bella et al., 2007, 2009, 2015; Loui et al., 2008), and confirm the existence of different phenotypes of rhythm disorders, resulting from either poor perception and/or deficient auditory-motor integration (Sowiński and Dalla Bella, 2013).

In the first reported case of beat deafness (Mathieu) it was hypothesized that this condition is the outcome of deficient beat perception (Phillips-Silver et al., 2011). Our findings, however, indicate that poor perception does not entail poor synchronization, and complement the dissociation showing poor synchronization in the presence of unimpaired beat perception already documented in patients with brain damage (Fries and Swihart, 1990; Provasi et al., 2014), and in healthy non-musicians (Sowiński and Dalla Bella, 2013). Notably, this finding does not preclude the possibility that in general beat perception and synchronization to the beat are highly coupled in individuals without rhythm disorders. Indeed, performance in perceptual and sensorimotor timing tasks is typically correlated (e.g., Keele et al., 1985). This link between perception and action may weaken, however, as a result of brain damage (e.g., cerebellar damage, Provasi et al., 2014; Schwartz et al., 2016) or of a developmental disorder (Sowiński and Dalla Bella, 2013).

To date, beat deafness has been associated with poor beat perception and with impaired sensorimotor mapping. As beat-deaf participants perform within the range of controls in pitch perception tasks requiring working memory or attention (e.g., from the MBEA; Peretz et al., 2003) these cognitive processes are supposedly spared. Yet, there is some recent EEG evidence indicating attentional deficits, in at least some cases of beat deafness. Mathias and collaborators (Mathias et al., 2016) showed a normal Mismatch Negativity to beat irregularities in beat-deaf participants, indicating unimpaired pre-attentive processing. However, one case of beat deafness (Mathieu) revealed abnormalities in later attentional processes (reduced P3b response to deviant tones). This finding suggests that attentional deficits relate to beat deafness.

It is intriguing that poor beat perception uncovered by a battery of explicit timing tasks (BAASTA; Dalla Bella et al., 2016) did not extend to an implicit timing task. The three beat-deaf participants were sensitive to the temporal regularity of a sequence, which facilitated the detection of a pitch difference in a reaction-time task. This finding points to some form of covert extraction of the beat, which is likely to afford synchronization. When moving to the beat listeners have to extract the beat of the stimulus to which they synchronize. If explicit beat tracking is not working properly, another mechanism has to provide the perceptual input needed to couple perception and action. A possibility is that different representations of durations are needed to track the beat, and to synchronize to it in explicit tasks. A representation of temporal duration built covertly may be sufficient to perform on an implicit timing task, and to provide perceptual input to support synchronization to the beat. This explanation, however, may not be as straightforward. Indeed, there is evidence suggesting that implicit and explicit timing rely on the same internal representation of duration (Piras and Coull, 2011). Another possible explanation is a deficit in the conscious access to the same internal representation. An intact internal representation of the beat, albeit not consciously accessible by L.A. and

L.C. in explicit timing tasks, may be processed covertly in order to afford synchronization. This explanation is compatible with the observation that all beat-deaf participants showed covert beat processing.

The finding that beat deafness is associated with spared implicit processing of temporal regularity shows that implicit processing of rhythmic properties of the signal is probably more robust than its explicit treatment. A similar dissociation was observed in other domains such as memory (e.g., Schacter and Graf, 1986), vision (Weiskrantz et al., 1974), and language (Ellis, 2005). Implicit timing has also been shown to be resistant to an interfering task (e.g., an auditory working memory task; Cutanda et al., 2015). Note that this distinction between implicit and explicit processing has also been investigated for pitch in patients with brain damage (Tillmann et al., 2007), or in congenital amusia (Omigie et al., 2012; Tillmann et al., 2012). For example, congenital amusics respond faster to notes with high probability than with low probability in the context of a melody (Omigie et al., 2012). This dissociation between explicit and implicit pitch processing in congenital amusia is supported by psychophysiological evidence. Individuals with congenital amusia, in spite of their severe deficits in treating pitch information in explicit tasks, show normal brain responses to small pitch changes (Peretz et al., 2009). It was concluded that in congenital amusia the neuronal circuitries needed to perceive fine-grained pitch differences are likely to be spared; yet, lack of awareness prevents them from accessing these differences in an explicit task. A similar explanation may apply to the rhythm dissociation described in the present study. This dissociation awaits further confirmation in a larger group of beat-deaf participants, and by comparing their performance in explicit and implicit tasks to that of the same control group.

Explicit and implicit timing mechanisms have been linked to separate neural substrates. A cortico-striato-cortical network has been associated with explicit timing (Coull and Nobre, 2008) while an inferior parietal-premotor network, linked to the cerebellum, was associated with implicit timing and temporal prediction (Coull et al., 2011; Coull and Nobre, 2008; Kotz and Schwartz, 2010; Nobre and Coull, 2010; Schwartz and Kotz, 2013; Zelaznik et al., 2002). It is possible that beat-deaf individuals recruit additional or spared neural pathways to compensate for impaired explicit timing. Consequently, impaired performance in explicit timing tasks may be associated with a malfunctioning network involving the pre-Supplementary Motor Area (pre-SMA) and the Basal Ganglia (BG) (Schwartz et al., 2012). Spared synchronization in L.A. and L.C. may be supported by motor areas (dorsolateral striatum, SMA proper) in addition to regions involved in implicit timing such as the cerebellum and left inferior parietal regions (Coull et al., 2011; Kotz and Schwartz, 2010; Schwartz and Kotz, 2013). These possibilities should be addressed in future studies examining brain responses and neural connectivity in beat-deaf individuals in both explicit and implicit timing tasks.

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